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Producing Seed Crops to Naturally Regenerate Southern Pines

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SUMMARY

Natural regeneration is a practical and inexpensive option for many existing southern pine forests, provided there is an adequate seed source and other stand conditions are controlled. However, seed production in natural stands of southern pines varies due to a wide range of environmental and biotic influences. It is important, then, to understand the biological processes that affect seed production in natural stands. The physiology of cone and seed production is reviewed here, and this information is applied to natural stand situations. With this knowledge, foresters will be better able to manipulate stands to improve and predict seed production and, therefore, make natural regeneration more reliable.

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INTRODUCTION

In recent years, emphasis has changed from clearcutting and artificial regeneration of southern pines to seed-tree, shelterwood, and selection harvesting methods, which rely on natural regeneration. This has raised several issues related to the potential success of these natural systems. One of the most critical is the adequacy of cone and seed production. During the last 30 to 40 years, Wakeley (1954) and numerous subsequent researchers focused on the cone and seed problems of regeneration by planting and seeding; little effort went into understanding these problems as related to natural regeneration.

Early research indicated great variability in the frequency of good seed crops of the major southern pines (USDA 1948)—loblolly (*Pinus taeda* L.), slash (*P. elliottii* Engelm.), shortleaf (*P. echinata* Mill.), and longleaf (*P. palustris* Mill.). The number of years a stand could bear adequate seed crops was documented to a limited degree in early publications (USDA 1948). But with current emphasis on extending rotation length on national forest land, there are still uncertainties about the effect of tree age on cone and seed productivity.

These and other questions related to the biology of cone and seed production in natural stands dictate that current knowledge about the processes of cone and seed production be applied to natural regeneration methods.

PERIODICITY OF SEED CROPS

Wakeley (1954) assembled data on seed production from a major survey of cone crops of the southern pines from Maryland to Texas from 1931 to 1941. He reported occasional years of heavy seed production by all species throughout most of the southern pine region. There also are years of widespread failure. Such general bumper crops and failures occur in no predictable pattern. Typically, however, cone production varies by species and locality, with good crops occurring every 3 to 10 years.

Loblolly pine is a moderate seed producer. It seeds abundantly near the Atlantic and gulf coasts but much less regularly in inland areas (McQuilkin 1940, Wakeley 1947). Seed crops of a 70-year-old stand in the North Carolina Piedmont ranged from 18,000 to nearly 300,000 seeds per acre during a 13-year period (Pomeroy and Korstian 1949).

Slash pine is a good seed producer, with heavy crops occurring about once every 3 years. However, because of its narrower geographic range, it may be more susceptible to complete crop failures (Wakeley 1954).

Seed production of longleaf pine is extremely variable from year to year and place to place. Some open-grown trees will bear cones every year, but good general crops are sporadic. During a 21-year period in south Mississippi, there were two heavy seed crops, seven medium, five light, and seven failures (Maki 1952). Boyer (1987) observed that the frequency of acceptable cone crops ranged from 3 years out of 4 to 0 over a period of 19 years. The frequency of good crops appeared to be lower nearer the gulf coast than farther inland. Many poor cone crops are due to causes other than lack of strobili.[1] In another south Mississippi study, abundant strobili appeared every year for 6 years, but only one good cone crop resulted (Allen and Coyne 1956).

Shortleaf pine is a less prolific seeder nearly everywhere; it is particularly poor along the western and northern edges of its ranges in the Ouachita and Ozark

[1] Female flower or strobilus refers to the reproductive bud from the time it becomes visible until pollination. Conelet refers to this structure from pollination until it starts enlarging in the second year; thereafter, the term cone is used.

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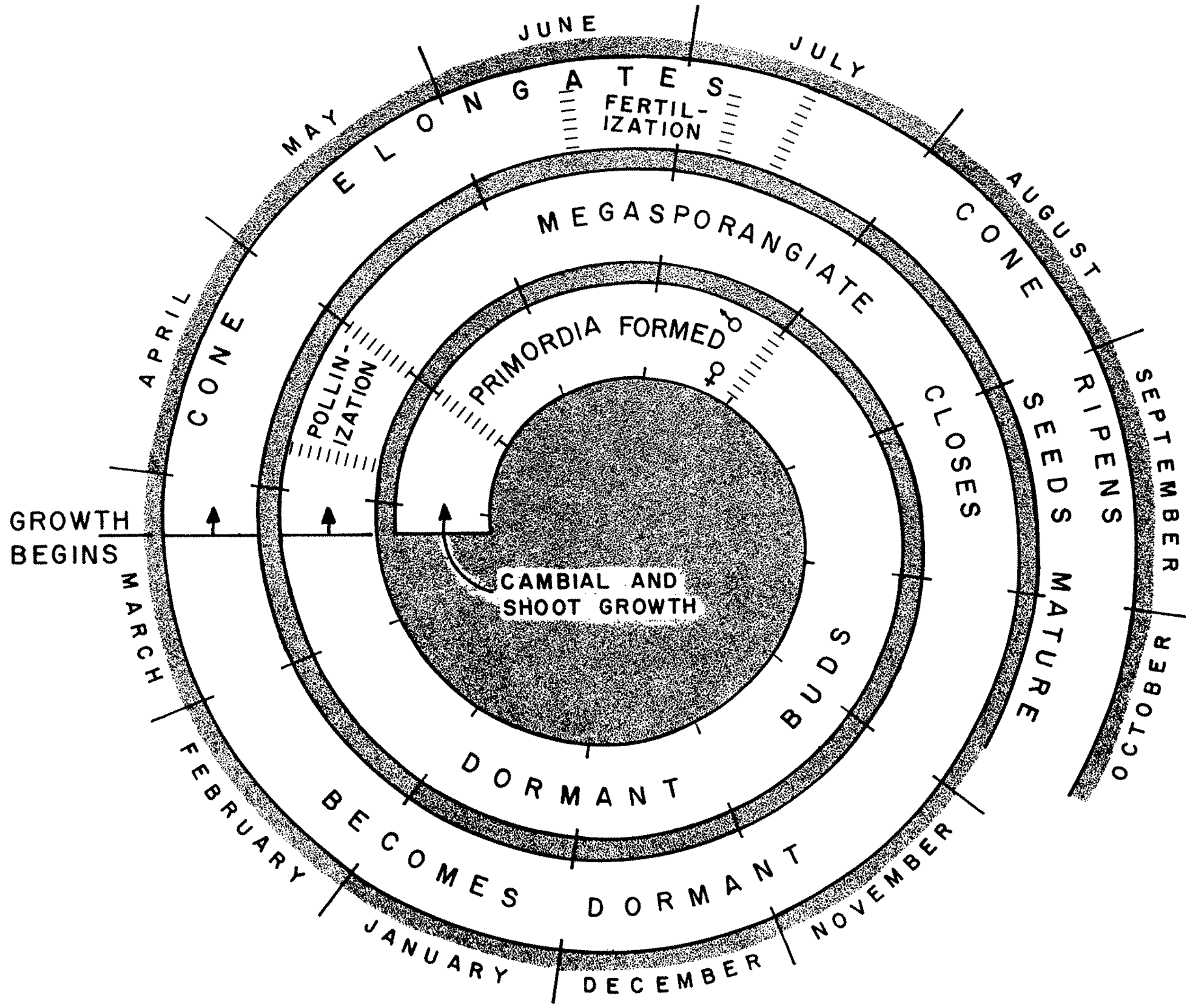

Figure 1. — *The pine reproductive cycle (adapted from Stanley 1958).*

Mountains of Arkansas and Oklahoma (Liming 1945). In most of its range, shortleaf may have adequate crops at intervals of 3 to 6 years (Grano 1965).

This variability in cone and seed crops seems unpredictable. However, by understanding the processes that affect strobili formation and the causes of losses during maturation, it should be possible to anticipate good years and to manipulate stands in order to produce more consistent seed crops.

PROCESSES THAT AFFECT STROBILI FORMATION

The first step in sexual reproduction in conifers is the initiation of flower buds or strobili. In southern pines, nearly 3 years occur between the time of strobili initiation and seed maturity (fig. 1). Strobili initiation begins in late July and August (Eggler 1961, Mergen and Koerting 1957), but female flowers do not become visible until midwinter. Initiation may occur any time during a 2-month period. Little is known about the chemical and physiological mechanisms of reproduction in trees. However, at least five factors contribute to flower induction: (1) induction hormones, (2) nutrient relationships, (3) soil moisture, (4) light conditions, and (5) temperature. These are briefly discussed in relation to southern pine seed production.

Flower-Inducing Hormones

As early as 1880, Sachs postulated that some special agent effective in flower production was induced under proper environmental conditions. Fraser (1958) stated that the physiological conditions of a plant during growth or flowering are probably controlled by small amounts of specific growth substances such as a florigen. One hint that a florigen might exist is the fact that in photoperiod-sensitive plants, something must transmit a flowering stimulus from the leaves to the stem tips, where initiation of primordia occurs (Kozlowski and others 1991). Growth regulators have been applied to try to increase cone production. Gibberellic acid, which has received research attention for the past 15 years, has occasionally stimulated cone production in conifers (Ross and Greenwood 1979). But these treatments have been used only in seed-production or orchard situations. Mechanical treatments such as girdling or strangulation have been used singly and in conjunction with gibberellic acid and have been more effective than chemicals alone in promoting flowering (Wheeler and Bramlett 1991). Mechanical treatments impede translocation of carbohydrates and hormones in the phloem. When downward movement of organic solutes is blocked, they tend to diffuse into the xylem and are translocated upward in the transpiration stream (Kozlowski 1971). Longman and Wareing (1958) demonstrated that bending branches from a vertical to a horizontal or downward position increased flowering of Japanese larch (*Larix leptolepis* Murray). This response to change in branch position is likely due to a change in organic solute diffusion. Neither application of growth regulators nor indirect methods such as mechanical injury are consistently effective for all southern pine species. Mechanical treatments may, in fact, be harmful over a period of years (Barnett 1993) and have little application to natural stands.

Nutrient Relationships

Minerals are involved in all major phases of reproductive growth, including initiation of primordia. Mineral requirements of reproductive growth are high, and a balanced supply ensures normal development of reproductive tissues, primarily by maintaining a large, physiologically active leaf surface, which in turn produces the metabolites and growth regulators required for development of strobili, cones, and seeds (Kozlowski 1971).

Hoekstra and Mergen (1957) applied 20 or 40 lb/acre of 7-7-7 or 3-18-6 nitrogen, phosphorus, potassium (NPK) fertilizers to 21-year-old slash pines in the spring. These treatments increased flower production an average of 59 percent over the controls. The 7-7-7 fertilizer was more than twice as effective as the 3-18-6 fertilizer, suggesting the importance of the nitrogen application rate. The effect of fertilization on flowering persisted for 2 years. This and other studies (Shoulders 1968) indicate that to stimulate flowering in southern pines, fertilizers should be applied in the early spring before strobili are formed. Fertilizers appear to mainly effect a single seed crop. Thus, continuous high production of seeds usually requires repeated fertilizer applications.

Shoulders (1967) treated longleaf pines with 15-25-10 NPK fertilizer annually for several years and found that flower production was stimulated in a complex manner, with rainfall and individual tree variables modifying the nutrient effect (fig. 2). In three stands in northeastern North Carolina, the loblolly pine seed crop was positively correlated with the May-to-July rainfall of 2 years earlier and negatively correlated with the size of the seed crop 2 years earlier (Wenger 1957).

Soil Moisture

Induction of flowering in southern pines is increased by high soil moisture during spring growth and lower moisture just before differentiation of strobili. For example, increases in February and March rainfall increased the response of slash pine flowering to fertilization, and high rainfall in April, or May through July, decreased it (Shoulders 1968). The results were somewhat different for longleaf pine. High rainfall in April, May, June, and July of the year before flowering greatly increased female flowering (Shoulders 1967), whereas wet weather through the entire growing season favored production of male flowers. As a result, large crops of female and male flowers did not necessarily coincide (Boyer 1981). Flowering varied by inherent flowering capacity, rate of fertilizer application, and rainfall during April and May.

Light

Although flower bud formation of many kinds of plants is affected by photoperiod, light intensity effects flowering of tree species more. Shirley (1936) reported that high light intensity favors fruit and seed production more than vegetative growth in several tree species. The higher flowering capacity is presumably due to the large amount of available carbohydrates resulting from high photosynthetic activity (Kramer and Kozlowski 1960). Fowells and Schubert (1956) reported that nearly all observed cones produced by ponderosa (*P. ponderosa* Laws) and sugar (*P. lambertiana* Dougl.) pines were borne on dominant trees, whereas only 1 to 1.5 percent were on codominant trees.

Within a tree crown, the vigor of branches also influences flowering and cone development. The more vigorous branches in the upper and middle two-thirds of the crowns of red pine (*P. resinosa* Ait.) produced more and larger cones than did the less vigorous branches of the lower one-third where the light level

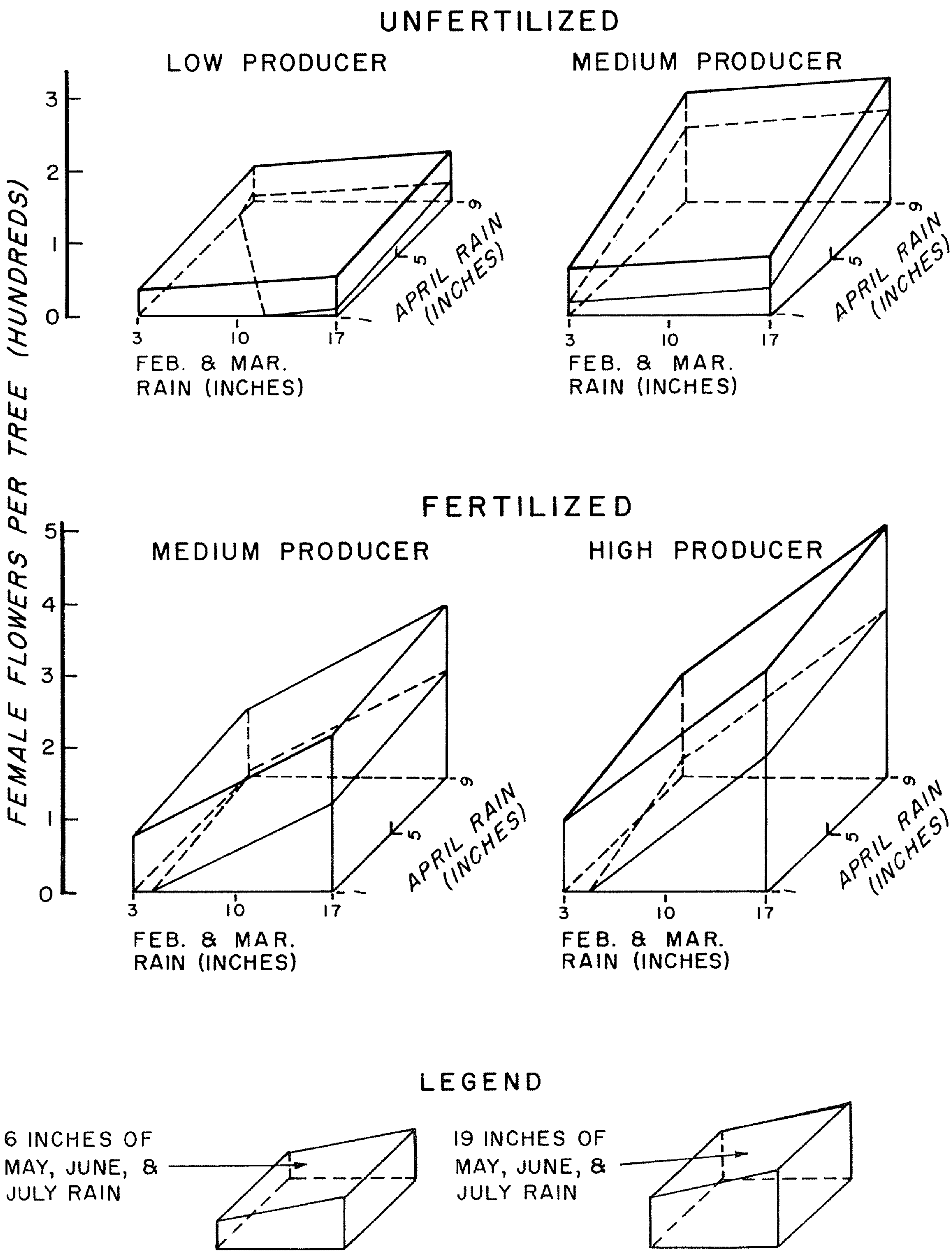

Figure 2. — *Effect of fertilizers and rainfall on estimated flower production of slash pine. Data are for low, medium, and high producing trees with different rates of fertilization and rainfall in the spring and summer preceding flower-bud formation. Average flower yields were assumed to be 30 per tree for low, 95 for medium, and 150 for high producers. Production 2 years earlier was set at 35, 105, and 1,751, respectively (adapted from Shoulders 1973).*

is much lower (Dickmann and Kozlowski 1971). Quality and quantity of seeds were also related to cone size. Cone volume increased with number of full seeds per cone, total dry weight of seeds per cone, and number of scales per cone (Dickmann and Kozlowski 1971). Increased cone and seed production following thinning of loblolly pine stands (Wenger 1954) further corroborates the importance of tree vigor to flowering and fruiting. Crown release is often followed by an increase in male flowers as well as female flowers, which increases pollen production and viable seeds per cone.

Temperature

Summer temperature has been found to affect seed and cone production of some species (Bramlett 1965, Fraser 1958, Lester 1967), but not specifically southern pines. Temperature has primarily affected flower development. Boyer (1978) used accumulation of degree-day heat sums to predict timing of southern pine pollen shed. Using a base of 50 °F and a starting date of January 1, accumulation of degree-days monitors the progress of flower development. However, this type of information is most useful for seed-orchard managers and others interested in pollen collection; it is not particularly useful for those managing natural stands.

STAND CONDITIONS AFFECTING SEED PRODUCTION

Once the processes of flower initiation and development are understood, it is easier to manipulate environmental conditions to favor cone and seed production. Stand density, nutrition, genetics, tree age and size, and topography are discussed in relation to processes that influence seed production.

Stand Density

Crown release or thinning is the most common and successful method known to stimulate flowering in forest trees. Thinning increases three of the variables essential to seed production: light, nutrients, and moisture. Although the higher light intensity probably exerts the greatest influence, the total response to release is undoubtedly due to a combination of these factors (Bilan 1960). Early observations of loblolly pine indicated that residual trees on cut-over areas produced more cones than did trees in uncut stands (Chapman 1923). Silvicultural practices were found to influence seed production—both shelterwood (Hebb 1955, Pomeroy and Korstian 1949) and alternate-strip

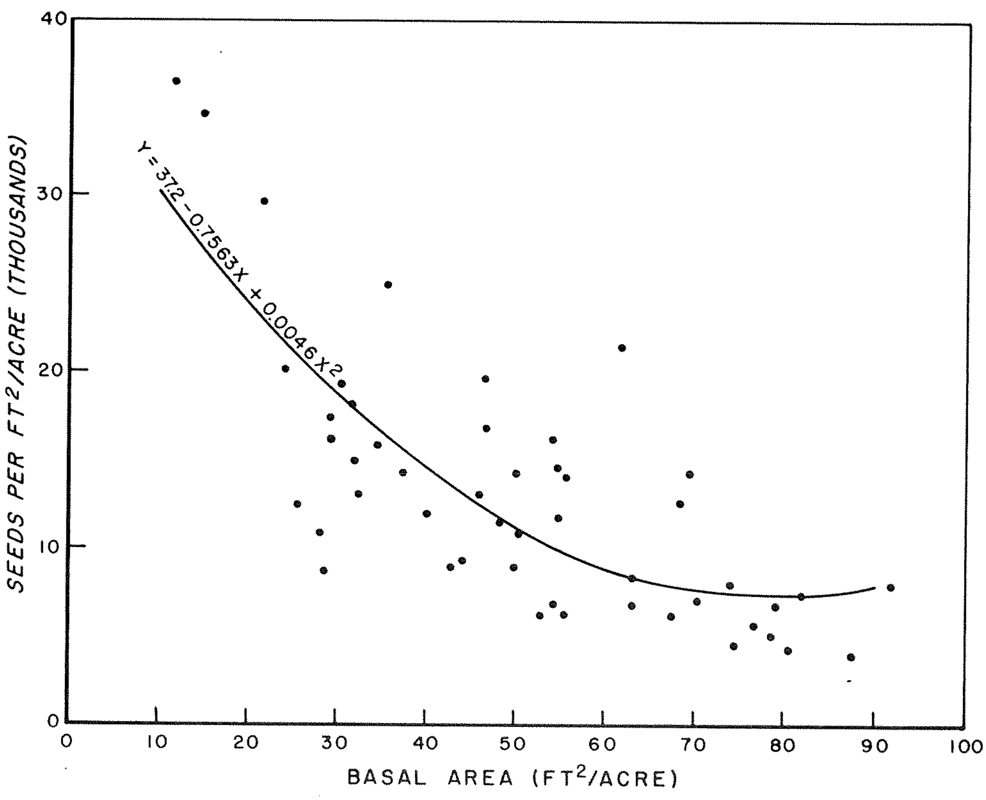

Figure 3. — *Four-year yield of viable seeds per square foot of loblolly-shortleaf pine seed-tree basal area in relation to stand basal area (adapted from Grano 1970).*

cutting (Trousdell 1950) increased the seed production of residual trees. Wenger (1954) determined that loblolly pine cone production on released trees was 7 to 10 times that of unreleased trees. Similar responses have been reported for longleaf pine (Allen 1953, Croker 1952), slash pine (Cooper and Perry 1956, Halls and Hawley 1954), and shortleaf pine (Phares and Rogers 1962).

Residual stand densities greatly influence quantities of seed produced. In a study of seed yield and quality in loblolly-shortleaf pine selection stands, Grano (1970) reported that production per square foot of basal area decreased curvilinearly with increasing basal area (fig. 3). Total and viable seed production increased with increasing basal areas up to 70 ft^2/acre and then declined. These results appear consistent with other southern pines. Boyer and White (1989) recommend that the preparatory cut of longleaf pine for shelterwood regeneration reduce basal area to a maximum of 70 ft^2/acre. Then, the longleaf pine shelterwood seed cut itself should reduce basal area to about 30 ft^2/acre. Particularly for longleaf pine, seedling establishment is improved with further reduction in stand densities.

Nutrition

The use of fertilizers in southern pine forests continues to increase, so it is not unreasonable to expect its use in stands at various times during their rotation. The compatibility of fertilization to increase cone and seed production and fertilization to promote growth has been questioned. Kramer and Kozlowski (1960) state that when trees are not nutrient deficient, adding large amounts of nitrogenous fertilizers may decrease seed production by increasing vegetative growth. However, most studies of fertilization of the southern pines show that moderate nitrogen applications in typical southern forest soils, usually low in nitrogen, do increase seed production. Fertilizing with large amounts of potassium (252 lb/acre) and phosphorus (180 lb/acre) with a moderate rate of nitrogen (120 lb/acre) doubled seed production in a 37-year-old natural shortleaf pine stand (Brinkman 1962).

Fertilizers are normally applied earlier in stand development than is needed for seed production; however, there is merit to an application late in the rotation that can stimulate development of newly established stands. Fertilizing while there is a crown canopy will reduce development of understory grasses and herbaceous plants that compete for nutrients and light and improve seedling response. Particularly where seed production is inadequate, fertilization could be considered both for seed production and seedling growth.

Tree Age and Size

Many stands may now be grown on rotations of 100 years or more because of environmental concerns and issues related to threatened and endangered species. Can these older trees produce adequate quantities of seeds to support natural regeneration?

A few studies have evaluated the effect of stand age on seed production. Barnett and McLemore (1961) found no differences in seed production or quality from longleaf pine stands ranging from 21 to 85 years. Wenger (1957) reported the results of a 7-year study of loblolly pine seed crops that involved one stand 95 years old and two others 145 years old. Advancing age apparently had no detrimental effect on seed production. All three stands produced from 50,000 to 800,000 seeds per acre annually. Lawson (1986) indicates that leaving very old (100 years or older), slow-growing shortleaf pines should be avoided. But if trees are vigorous, there is probably no age limitation.

Croker and Boyer (1975) state that longleaf pine cone production by individual tree is affected by site quality, stand density, tree size, and genetic predisposition. The best producers are dominant trees 15 inches or more in diameter, with large crowns and a history of past cone production, as evidenced by old cones under trees. A longleaf pine tree 15 inches in d.b.h. will produce, on the average, more than twice as many cones as a 12-inch tree, and a 19-inch tree, more than twice as many cones as the 15-inch tree (Boyer and White 1989). But, for a given basal area, per-acre cone production is not greatly changed by increasing tree size above 15 inches in d.b.h., as the increase in cone production per tree is largely offset by the reduction in number of trees per acre.

Wakeley (1954) stated that southern pine cones should not be rejected because of tree age. Pines of 7 to 15 years produce seeds of good quality, and excellent seeds have been collected from 280-year-old shortleaf pines and 350-year-old longleaf pines. Once trees have reached seed-bearing age, seed production rarely declines with advancing age, provided that the trees remain healthy and vigorous (Smith 1962).

Genetic Predisposition

Fruitfulness is hereditary to some degree, and cone crops of individual trees are closely related to past production (Pomeroy 1949, Wenger 1954). Croker (1964) found that over a 5-year period, longleaf pine cone production was influenced more by inherent fruitfulness of individual trees than by fertilization and irrigation. It is important, then, when sufficient trees are available, to select residuals based on past cone production as well as other criteria. This can be done by observing the numbers of cones both on trees and on the ground under individual trees.

Topography

Topography usually does not affect seed production on most sites across the South. However, in mountainous areas, such as the Ouachita and Ozark Highlands, slope and aspect can strongly influence seed production. Air temperature at the base of slopes may be 5 to 12 °F cooler than a few hundred feet up the slope (Hungerford and Babbitt 1987). Aspect also greatly influences temperature, light, and soil moisture conditions. South- and west-facing slopes are warmer and drier than the north- and east-facing slopes due to greater exposure to sunlight. These environmental differences affect species distribution and also cone and seed production. The specific responses to topography will vary by location, species, and climate, but slope and aspect are important considerations in managing natural stands. For example, the female strobili on pines on the lower portions of north-facing slopes may frequently be subjected to freeze injury.

POTENTIAL LOSSES DURING THE MATURATION PROCESS

Early initiation of large quantities of female strobili does not necessarily guarantee production of good seed crops. Of nearly 28,000 strobili tagged on selected clones of the 4 major pine species over 4 years, only 41 percent developed into cones (McLemore 1977). Others have noted that when abundant strobili were produced on longleaf pines each year over a 6-year period, only one good cone crop resulted (Allen and Coyne 1956). Several factors are responsible for these losses.

Insect and Animal Damage

Most losses during maturation are caused by insects. McLemore (1977) attributed 98 percent of the strobili and conelet losses of the four major species in a Louisiana seed orchard to insects. Losses over the 4-year period of the study were higher in shortleaf and longleaf pines than loblolly and slash pines. In a study of shortleaf pine, Bramlett (1972) reported that overall survival from flowering to the mature cone stage varied annually from 3 to 65 percent and averaged 29 percent over a 6-year period. Major losses were attributed to insects. DeBarr and Ebel (1974) and Ebel and Yates (1974) also reported high losses of southern pine conelets due to insects. Most losses are caused by *Dioryctria* spp., but several other insects are involved at various stages of development. Losses, as a percentage of the total crop, are particularly heavy during poor seed years. Also, insect populations and damage tend to build if there are several consecutive years of medium to good cone production.

Losses due to animals such as squirrels are a problem in localized areas. Bramlett (1972) reported that squirrels reduced maturing cones by 42 percent between July and September during 1 year of a 6-year study. Again, the problem seems to be most serious when crops are poor.

Weather-Related Injury

The primary weather-related losses are spring frosts during flowering, extended droughts, and isolated occurrences such as hail. Temperatures of 25 to 28 °F severely damaged developing female flowers of shortleaf pine, whereas undeveloped flowers protected by bud scales escaped with little damage (Campbell 1955). A late-season freeze killed 30 percent of female flowers on a sample of 23 shortleaf pines in the Virginia Piedmont (Bramlett and Hutchinson 1964). In both of the above instances, juvenile foliage on several hardwoods was also damaged. Apparently, frost injury to hardwood leaves may forecast poor pine seed crops. Frost damage occurs most frequently on the north slopes of the mountainous portions of a species' range where temperature fluctuations are great.

Losses due to hail, drought, and wind storms occur infrequently. In localized areas, these factors can significantly reduce cone production. McLemore (1977) reported that an April hail storm broke branches bearing 20 percent of the female flowers in 1 year of 4 studied.

FORECASTING SEED CROPS

The most common way to predict seed crops in advance of cone maturity is by evaluating flowers or immature cones. Although procedures for predicting seed crops 20 months in advance of maturity, based on estimates of female flowers, have been developed for southern pine seed orchards (Fatzinger and others 1988), binocular ground counts of flowers are unsatisfactory estimators of seed production in forest stands (Shoulders 1968). Croker's (1971) research on estimating flower crops of longleaf pines indicated that flowers are highly visible for only about 2 weeks between early flower development and growth of the needles. During this short period, a factor of 1.5 can be used to estimate total numbers of flowers; outside of this period, flowers could not be reliably predicted. Under stand conditions, these estimates do not adequately predict cone and seed production nearly 2 years later.

Wenger (1953) estimated the number of maturing loblolly pine cones in late summer with reasonable accuracy by counting visible cones through binoculars from a single vantage point and doubling the number. Binocular counts made in midsummer on only 4 to 5 percent of loblolly pines in a seed orchard provided good crop estimates (Wasser and Dierauf 1979). Webb and Hunt (1965) used a similar approach to estimate cone crops in a slash pine seed production area with success. Seidel (1970) successfully used a two-person counting system in a 40-year-old shortleaf pine seed-production area. The numbers of sound seeds per cone may vary between years (McLemore 1975), and it is advisable to estimate this number as well as the number of cones (Bramlett and Hutchinson 1964). Techniques to predict numbers of seeds per cone and cones per bushel are well documented (McLemore 1962, 1972).

Trousdell (1950) described a method of forecasting annual variations in loblolly pine seed crops in natural stands. The procedure consists of counting the previous-, current-, and next-year's cones on sample branches obtained from felled trees. This technique assumes that the relative seed yield from the old cones is known and the increase or decrease in the number of cones measures the expected change in seed crops. Read (1953) applied the method to shortleaf pine and found regeneration success was closely related to the seed crops forecasted by this technique.

Technology now exists to improve the quality of these predictions. Solar-powered, automated weather stations are frequently used to monitor the weather conditions at research sites. Brissette and others (1992) report on the types of environmental data collected over a several-year period at a remote site in the Ouachita Mountains of Arkansas. Installing such equipment in natural stands where regeneration is expected could provide data to verify rainfall, temperature, and light relationships that have affected seed production in earlier studies. Increasing knowledge of these relationships should provide silviculturists and land managers the means to forecast seed crops in time to prepare the site and complete other tasks in anticipation of good seed crops.

CONCLUSION

Seed crops in natural southern pine stands vary greatly according to environmental and biotic influences. This variability lowers the reliability of natural regeneration in these stands. Applying knowledge of physiology of flower initiation and cone and seed production should help foresters better manage stands to increase seed production. A better understanding of the biology of production should also improve their ability to forecast seed crops.

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The biological processes that affect seed production in natural southern pine are documented, and information that will allow foresters to manipulate stands in a manner to improve and predict seed production is provided. As a result, natural regeneration should become a more reliable technique.